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Notes on the fruits of some species of Opuntia

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(With plates 9 and 10)

In the study of the species of *Opuntia* in the field, one is continually impressed by the correlation between structure and environment. The genus is, evidently, of comparatively recent origin and development. As yet no one has been able to make a satisfactory taxonomic disposition of the various species. This, evidently, is largely due to the instability of the characters which the systematist must use to separate the multiplicity of forms which comprise the genus.

A few species are known from humid regions. The genus as a whole is a desert type. Between 90 and 100 species and varieties have been described from the southwestern United States and northwestern Mexico, where they grow under the most arid conditions.

The correlation between the various organs of these plants and the environmental conditions under which they have developed is of great interest, not only to the morphologist but to the student of physiological botany as well. The fitting of form and structure to function under a desert environment has resulted in the development of organs along different lines and with different uses from those of the homologous organs of plants of more humid regions. In order to facilitate nutrition, dissemination, protection, and reproduction, under the adverse environmental conditions where the plants grow, both structure and function are highly specialized.

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In all species the shoot is more or less condensed and fleshy. The roots are also occasionally fleshy, as in *O. macrorhiza* and *O. filipendula*. More frequently the roots are of two sorts, long surface ones for the rapid absorption of moisture, and short deeper ones to give the plant support. The former are of quite different structure from the latter. In many species the fruit has developed along special and circumscribed lines.

Opuntia fulgida is often a tree in habit and size, and grows best in the most arid situations in southern Arizona. It seldom reproduces by natural seeding, depending almost entirely upon vegetal dissemination for its reproduction. In this species the fleshy, proliferous fruits grow in large, pendulous clusters. They are like short vegetative branches, and have few or no spines (FIG. 1). These large fruit-clusters are often sterile, and under the adverse environment the seeds that do develop usually fail to grow. The species, however, has become rapidly and widely spread through vegetal dissemination.

The fruit is usually most abundant on the lower branches and is within easy reach of cattle and other animals. Where undisturbed it remains on the trees for many months after maturing, but because of its succulency and lack of spines it is sought after by wild as well as domestic animals. In this species the ultimate branches are very succulent, densely covered with spines, two inches or less in diameter and four to eight inches long. They are very fragile, becoming detached from the plant with the slightest disturbance. Animals, in their effort to get the fruit, come in contact with them. The fragile branches become detached and adhere to the animals like large burs, finally to fall to the ground, often after being carried for miles. The basal end of the branch usually comes in contact with the soil because of the few short spines at this end, roots rapidly develop, often in the driest of weather, and a new plant becomes established.

The spineless nature of the fruit, its succulency, its growing in large clusters, its remaining attached to the plant for months after maturity and its position within easy reach of cattle and other large animals, are all important factors in vegetal dissemination. I believe that the special acquired function of the fruit as an aid in vegetal dissemination is gradually influencing its character and

form. It is certainly changing from its original seed-bearing condition to one of sterility.

Plants of this species are occasionally observed bearing clusters of short spineless branches which externally closely resemble the clusters of proliferous fruits. These clusters of branches serve the same purpose as the fruits in attracting animals. It is possible that they have developed because of the intimate relation between animal life and vegetal dissemination. The fruit is caulome in structure and through its specialized use is gradually becoming sterile. In instances where the flowers have failed to develop we find these clusters of short fruit-like branches. They differ from the ordinary ultimate branches only in form, size, and want of spines.

In a number of species, specialized branches are developed which are themselves disseminated, *i. e.*, they do not aid in the dissemination of the normal ultimate branches as in *O. fulgida*. In *O. tetracantha*, *O. leptocaulis*, *O. arbuscula*, and other species with long, slender shoots, the wand-like branches are not fragile. They are not readily detached from the plant and they are not disseminated through the agency of animals. Each of these species, however, develops many short, tumid, specialized branches (FIG. 2a and FIG. 3a) but little longer than the fruits. These branches become readily detached, develop roots and form new plants on coming into contact with the soil. Large numbers of these specialized branches develop during dry and adverse seasons. Under more favorable conditions they are almost entirely replaced by fruit.

From the study of the fruit of many species of *Opuntia* from the standpoint of structure, from the similarity in external appearance between the fruit and the ultimate vegetative branches and from teratological evidence as illustrated later in this paper I have been led to the following conclusions:

1. The fruit of *Opuntia* is caulome in structure.

2. Its caulome nature is probably of recent development.

3. It has become caulome by its once superior ovary receding into a vegetative branch, thus making it at present inferior.

4. The branch, which now becomes the ovary, is usually modified and ripens into the structure which we term the fruit; it may however become but little modified, resembling the ultimate branches and continuing as a vegetative part of the plant.

The usual form of the fruit of *Opuntia versicolor* is pear-shaped (FIG. 4). It usually contains a number of well-developed, fertile seeds. It is occasionally sterile, and not infrequently shows no vestige of a seed-cavity (FIG. 5). Sometimes on the same plant with the forms of fruit mentioned above are found structures which resemble the ultimate branches in almost every respect with the exception that there is a seed-cavity containing fertile seeds in the upper end (FIGS. 6, 7, 8). Are all of these structures fruit? In this case there seems to be no dividing line between vegetative branch and fruit. The seeds in developing within the branch have influenced only its upper end. Such branches, although they contain seeds, continue indefinitely as a vegetative part of the plant; often the only external evidence indicating the fruit-character of these structures is the presence of the umbilicus at the upper end.

Throughout the genus *Opuntia* the fruit in its early development bears numerous leaves in the axils of which vegetative branches as well as flowers may occur (FIGS. 1 and 9).

The fruit of the flat-stemmed species of *Opuntia* deviates farthest in form from that of the normal vegetative branch. In *O. Engelmanni* the fruit is usually more or less pear-shaped (FIG. 10). In this species as well as in a number of other flat-branched forms, the structure containing the seeds is sometimes large and flattened like the normal vegetative branches (FIG. 11). In such cases, however, the whole member does not become pulp-like, change color, and ripen in the fall. Only that part immediately surrounding the seeds "ripens" as the seeds mature, the remainder continues as a vegetative part of the plant. When the fruit is sterile it often does not ripen at all but remains on the plant for months after the normal fruits have matured. These sterile fruits occasionally produce normal flattened branches (FIG. 12) during the second season.

The following teratological evidence suggests that the present caulome structure of the *Opuntia* fruit is a successive development from what was formerly a phyllome structure. In the sterile fruit of *O. Engelmanni* (FIG. 13) there is no evidence whatever of a seed-cavity. In this fruit the style persisted for several months after the flower appeared and continued to grow until it reached a diameter several times that of the style in the normal flower. It

became red in color in the late fall, like that of the normal fruit, and developed a central cavity which contained a large number of abortive ovules. In all species of *Opuntia* the large, thick style has a much swollen base; it is possible that this is the last remnant of what was once the seed-receptacle.

The adverse environmental conditions under which *Opuntia* grows is ample reason for this interesting evolution. The ovary, which possibly at one time was superior, has gradually become more and more depressed until now it is entirely enclosed in the fleshy branch.

YALE FOREST SCHOOL.

Explanation of plates 9 and 10

PLATE 9

FIG. 1. *Opuntia fulgida;* cluster of the proliferous fruits: *a*, fruits with fertile seeds and of the usual pear-shaped form; *b*, fruit much elongated, spinescent, and resembling a vegetative branch. $\times \frac{2}{9}$.

FIG. 2. *Opuntia tetracantha;* section of a long, slender branch bearing a short branch and fruit: *a*, one of the short specialized branches which usually become detached at the end of the first season. $\times \frac{1}{3}$.

FIG. 3. *Opuntia arbuscula;* short section from a long, slender branch bearing a short specialized branch (*a*), and a flower (*b*). $\times \frac{1}{3}$.

FIG. 4. *Opuntia versicolor;* normal pear-shaped fruit. $\times \frac{1}{3}$.

FIG. 5. *Opuntia versicolor;* sterile fruit. $\times \frac{1}{3}$.

FIGS. 6, 7, 8. *Opuntia versicolor;* structures resembling the normal vegetative branches in external appearance, but containing the seed-cavity with perfect seeds at the apex. $\times \frac{1}{3}$.

PLATE 10

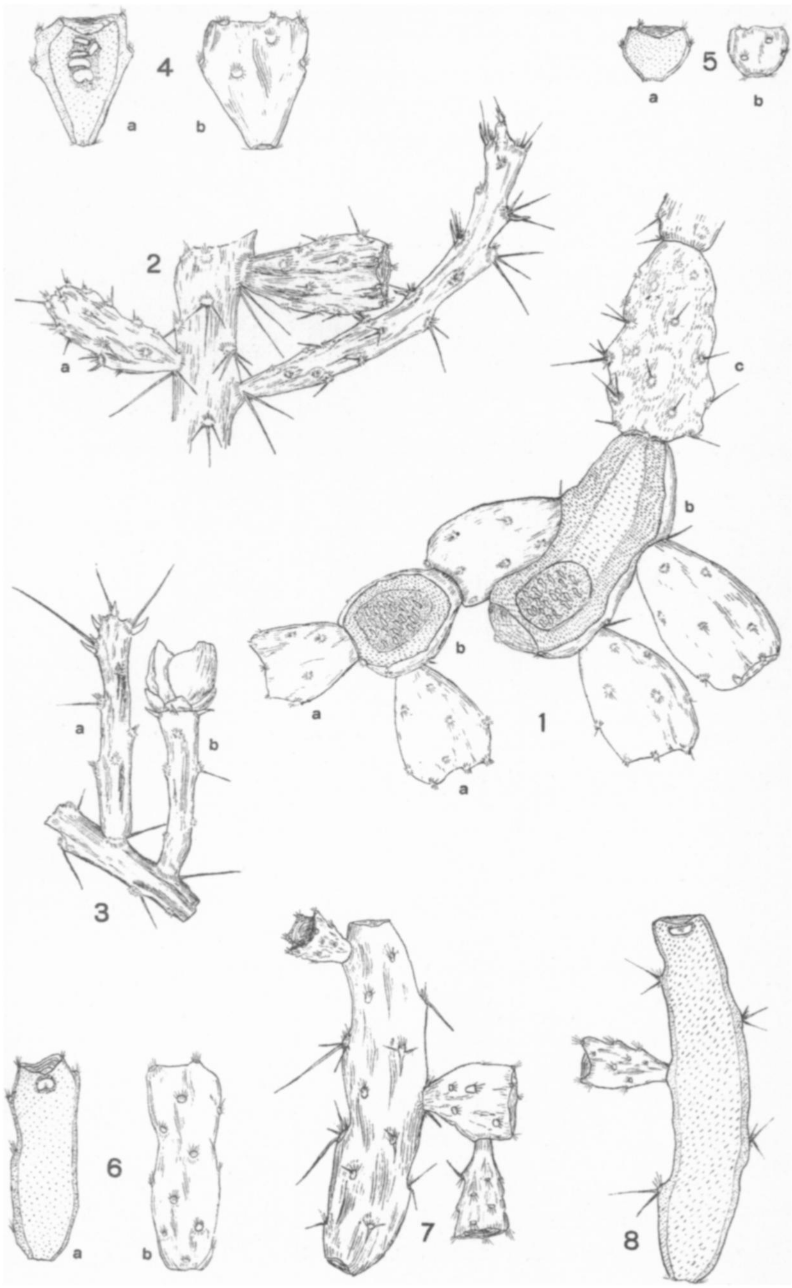
FIG. 9. *Opuntia leptocaulis;* a fruit bearing two long branches, one of which is floriferous. $\times \frac{1}{3}$.

FIG. 10 *Opuntia Engelmanni;* normal pear-shaped fruit. $\times \frac{1}{3}$.

FIG. 11. *Opuntia Engelmanni;* the seed-cavity with perfect seeds in the apex of a flattened branch. $\times \frac{1}{6}$.

FIG. 12. *Opuntia Engelmanni;* a sterile fruit persisting until the second year and from which is growing a normal flattened branch. $\times \frac{1}{6}$.

FIG. 13. *Opuntia Engelmanni;* a sterile fruit on which the style has persisted, continued in growth, and formed a central cavity in which are many abortive ovules.



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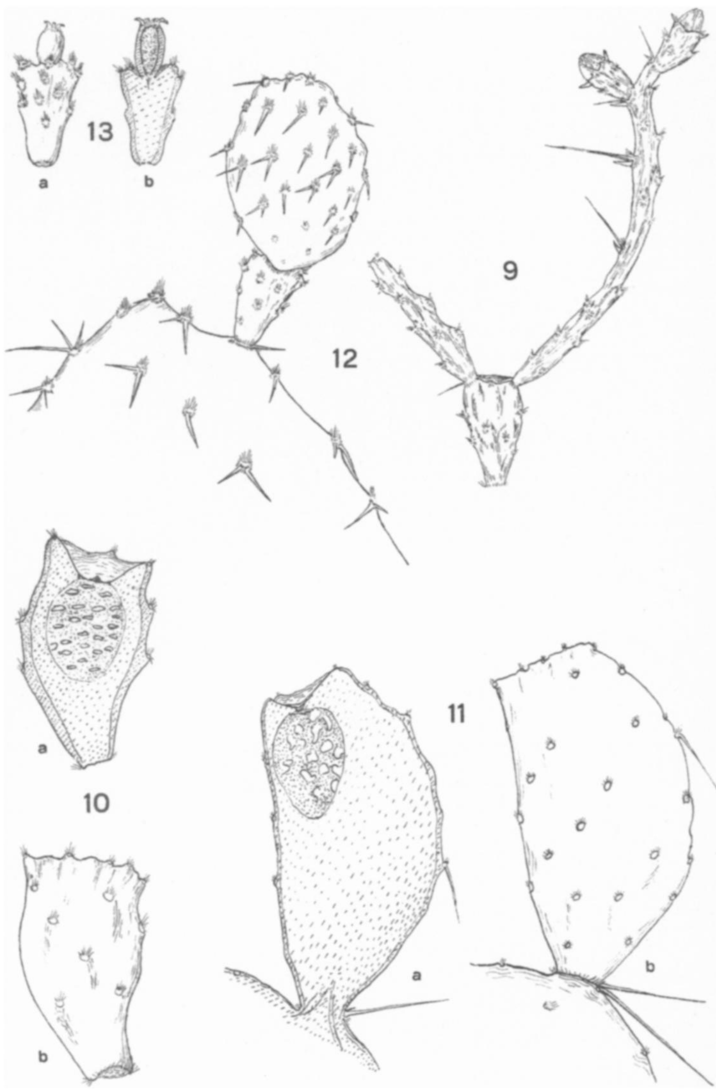

FRUITS OF OPUNTIA.